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RESEARCH LETTER

Contrasting patterns of change in the distribution and abundance of farmland birds in relation to farming system in lowland Britain

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ABSTRACT

Patterns of change in distribution (presence/absence) and abundance since the late 1960s were examined in 20 species of farmland bird in southern Britain in predominantly arable (eastern), predominantly mixed (central) and predominantly grassland (western) regions. Comparisons were made between changes in distribution and in abundance to determine whether these measures show similar relationships to environmental change. Local extinctions of selected species and reductions in species richness were significantly greater in the predominantly grassland region. Decreases in abundance were greatest in seven species in the predominantly arable region, two in the mixed region and nine in the grassland region. Changes in distribution and abundance showed consistent patterns in three species, turtle dove *Streptopelia turtur* L., yellow wagtail *Motacilla flava* L. and reed bunting *Emberiza schoeniclus* L. In another four species, grey partridge *Perdix perdix* L., lapwing *Vanellus vanellus* L., tree sparrow *Passer montanus* L. and corn bunting *Miliaria calandra* L., decreases in abundance were greatest in the arable region, yet declines in distribution were lowest. For other individual species, changes in distribution were too small to draw any conclusions in relation to farm type. We suggest that modern grassland systems are suboptimal habitats compared to arable or mixed agricultural land for many farmland species that occur at relatively low density in the more western, grass-dominated region. Declines in abundance are therefore more likely to lead to local extinction in these areas than in eastern areas where abundance is higher. However, the role of changes in grassland management on bird populations requires further research. It is suggested that conclusions drawn from changes in distribution alone, in the absence of supporting data on changes in abundance, may be misleading where the aim is to assess how large-scale spatial dynamics of populations relate to environmental change.

Key words Abundance, farmland birds, grassland agriculture, macroecology, population declines, southern Britain, species distribution, species richness.

INTRODUCTION

Macroecological relationships between local abundance and distribution or range size have recently received much attention (Gaston & Lawton, 1990; Lawton, 1996; Gregory & Blackburn, 1998). Increasingly, large-scale distributional data are being used to explore spatial relationships between species occurrence and environmental factors, and to gain insights into the role of factors such as land-use change in determining distributional change (Donald & Fuller, 1998). A premise of such studies is that distributional changes will broadly parallel abundance changes, but this has been rarely tested. It is unclear how the conclusions drawn from these studies will compare with those from finer-scale work on factors affecting change in local abundance. In this paper we demonstrate that distributional change and abundance change in birds can show strikingly different patterns with respect to agricultural habitat type. To our knowledge, this is the first demonstration of such patterns in birds.

The decline in population size and contraction in range of a number of northern European farmland bird species over the past 20–30 years has been well documented (Marchant *et al.*, 1990; Hustings, 1992; Gibbons *et al.*, 1993; Tucker & Heath, 1994; Fuller *et al.*, 1995; Siriwardena *et al.*, 1998). Fuller *et al.* (1995) report that of 28 species associated primarily with farmland in the UK, 24 have shown a contraction in range, and 15 of 18 species that could be censused accurately showed a decrease in population size between the late 1960s and early 1990s. These declines were far greater than for species associated with other habitats, such as woodland, uplands or wetlands, over the same period. Apart from their association with farmland, these species are ecologically diverse. Over the same period, there have been major changes in many aspects of agricultural management (Grigg, 1989; Stoate, 1996). Many components of farming systems have changed more or less simultaneously in the last 30 years, making it difficult to identify individual factors (whether agricultural or otherwise) which may have driven population declines (Chamberlain *et al.*, 2000). For example, Chamberlain & Fuller (2000) considered the relationships between a range of agricultural management variables and the change in bird distributions in Britain. A large number of variables had a similar spatial and temporal pattern of change leading to a high level of collinearity in the data, therefore it was difficult to identify individual factors that were most likely to have affected bird distributions.

Lowland farmland in Britain shows strong regional differences. Arable systems tend to dominate in the east and grassland systems tend to dominate in the west. This regional divergence has become more pronounced over the last three decades. Comparison of distributional population changes in different regions defined by farming type can be extremely informative about the processes that may be involved. Two previous examples of this approach can be given. Marchant & Gregory (1994) found that granivorous passerines tended to show the steepest population declines on arable farmland sites and in regions associated with arable farmland, thus implicating changes in arable management as a cause of the national decline. Similarly, Gregory & Marchant (1996) found that a number of corvid species showed the greatest increases in density on grassland and mixed farmland, implicating changes in grassland management as a potential cause of population increase.

We consider changes in the populations of common farmland bird species, both in terms of abundance (from long-term census data) and distribution (from atlas data), in lowland farmland in England and Wales in different regions defined according to predominant farming type. The aims of the paper are twofold: (i) to determine whether species declines are associated with particular types of farming system; and (ii), to determine whether consistent patterns are shown between population change measured in different ways, i.e. whether local extinctions (atlas data) are consistent with changes in abundance (census data) across regions.

METHODS

Regions of predominant farming type

Data were derived by the Edinburgh University Data Library from parish summaries of the Agricultural June Census carried out by the Ministry of Agriculture, Fisheries and Food (MAFF). These were used to define predominantly arable, mixed and grassland farming regions in England and Wales defined at the county level. Counties defined as arable were those where arable farmland occupied over 10 times the area of grassland in 1988, counties defined as grassland were those where grassland area occupied over 10 times the area of arable land, and counties defined as mixed were intermediate. The geographical location of the regions is shown in Fig. 1. A previous analysis of trends in individual agricultural variables demonstrated that changes in the area of crops and grass and in the numbers of livestock at the 10-km square level had shown very similar patterns within each region (Chamberlain & Fuller, 2000), so each region is representative of different broad-scale changes in agriculture.

Bird data

The distribution of all breeding bird species in Britain and Ireland has been estimated by visiting every 10-km square of the national grid in two Breeding Bird Atlas surveys, first between 1968

Fig. 1 The distribution of predominantly arable (black), mixed (shaded) and grassland counties in England and Wales. Lines show county boundaries. Counties with over 90% of agricultural area covered by either arable or grassland were classified accordingly. Counties with intermediate areas of grass and arable were classified as mixed (data derived from MAFF Agricultural June Census).

and 1972 (Sharrock, 1976), and secondly between 1988 and 1991 (Gibbons *et al.*, 1993). These data were used to determine the loss (local extinction), retention or gain (local expansion) of a species from 10-km squares in England and Wales between 1968 and 1972 (referred to as the early period) and 1988 and 1991 (referred to as the late period). Additionally, the change in species richness (i.e. number of species present) per 10-km square was analysed, concentrating mainly on a group of 20 target species selected on the basis of the quality of the available data and whether the species was considered characteristic of lowland farmland in England and Wales (Fuller *et al.*, 1995). The species selected were kestrel *Falco tinnunculus* L., grey partridge *Perdix perdix* L., lapwing *Vanellus vanellus* L., stock dove *Columba oenas* L., turtle dove *Streptopelia turtur* L., skylark *Alauda arvensis* L., yellow wagtail *Motacilla flava* L., starling *Sturnus vulgaris* L., whitethroat *Sylvia communis* Latham, blackbird *Turdus merula* L., song thrush *T. philomelos* L., tree sparrow *Passer montanus* L., chaffinch *Fringilla coelebs* L., bullfinch *Pyrrhula pyrrhula* L., greenfinch *Carduelis chloris* L., goldfinch *C. carduelis* L., linnet *C. cannabina* L., corn bunting *Miliaria calandra* L., reed bunting *Emberiza schoeniclus* L. and yellowhammer *E. citrinella* L. As we were concerned only with lowland farmland, squares which had less than 50% total agricultural area in 1988 (derived from MAFF June census data) were not considered (so squares with large amounts of urban land, woodland or uplands were not included).

The Common Birds Census (CBC) is a long-term monitoring scheme, running since 1962, which provides relative annual population estimates of a large number of British bird species (Marchant *et al.*, 1990). Estimates of relative population change and change in breeding density were derived from CBC data for 20 target species typical of lowland farmland in England and Wales. The CBC involves volunteer observers visiting census sites 10 times during the breeding season to determine the number and location of all bird territories using a territory mapping method. Full survey methods can be found in Marchant *et al.* (1990). The data are used primarily to calculate population indices that reveal relative changes from year to year, hence providing an estimate of population change. CBC indices were determined from 522 farmland CBC sites in England and Wales with an average area of 71.4 ± 33.0 SD hectares. Not all of these sites were covered every year, only ≈ 100 sites being censused annually. As CBC sites are not randomly distributed, estimates of change from the entire CBC data set may be unrepresentative of the United Kingdom as a whole, the distribution of sites being biased towards arable farmland in south-east England (Fuller *et al.*, 1985). Deriving indices from different regions overcomes this bias.

Analyses

The number of 10-km squares occupied in both atlas surveys was determined for all species and simple comparisons of local extinctions in different regions defined using agricultural statistics were carried out. The number of 10-km squares where a bird species was lost and the number of 10-km squares where a bird species was gained or retained between the two atlas surveys was determined. The number of gains was very small (< 5%) in the majority of species, so it mattered little that they were not analysed separately. The exceptions to this were corn bunting and yellow wagtail, where local expansion was considered in a separate analysis; 10-km squares where a species was not recorded in either survey were not considered in the analysis.

CBC population indices were determined using log-linear Poisson regression, a technique which involved modelling logarithms of bird counts using the software TRIM (ter Braak *et al.*, 1994; Pannekoek & van Strien, 1996). Relative population changes were determined between 1970 and 1990 (coinciding with the distributional data), where 1970 was set as the reference year with an index of 100%. Siriwardena *et al.* (1998) had previously

Table 1 The percentage change in occupied 10-km squares between the two Atlas periods (1968–72 and 1988–91) for 20 selected farmland bird species in England and Wales, and in regions of predominantly arable, mixed and grassland agriculture; 10-km squares where a species was absent in both periods were omitted. Sample sizes (in brackets) indicate the number of occupied 10-km squares in the earlier period. Species showing significant differences are shown first. ** $P < 0.01$, *** $P < 0.001$ (G-test)

Total 10-km squares	Overall change 1089	Arable 298	Mixed 512	Grassland 279
Grey partridge	−13.9 (1039)	−10.5 (296)	−9.2 (502)	−27.8 (241)***
Lapwing	−7.2 (1064)	−2.7 (295)	−2.9 (512)	−21.0 (257)***
Turtle dove	−19.2 (918)	−0.3 (297)	−21.8 (473)	−48.6 (148)***
Yellow wagtail	−5.9 (777)	6.1 (245)	−10.8 (400)	−13.6 (132)***
Tree sparrow	−11.2 (948)	−5.1 (295)	−15.5 (484)	−9.5 (169)***
Corn bunting	−14.4 (725)	−7.1 (253)	−11.5 (353)	−38.5 (117)***
Reed bunting	−5.9 (1044)	−3.7 (298)	−4.7 (488)	−10.9 (258)**
Kestrel	−1.5 (1080)	0.7 (293)	−0.2 (511)	−6.2 (276) NS
Stock dove	−1.1 (1056)	−3.7 (298)	0 (501)	−0.4 (257) NS
Skylark	−0.2 (1088)	0 (298)	0 (511)	−0.7 (279) NS
Starling	−0.2 (1087)	0 (298)	0 (512)	−0.7 (279) NS
Whitethroat	−1.4 (1089)	−0.7 (298)	−1.4 (512)	−2.2 (279) NS
Blackbird	0 (1089)	0 (298)	0 (512)	0 (279) NS
Song thrush	0 (1089)	0 (298)	0 (512)	0 (279) NS
Chaffinch	0 (1089)	0 (298)	0 (512)	0 (279) NS
Bullfinch	−2.7 (1082)	−4.4 (294)	−1.6 (510)	−2.9 (278) NS
Greenfinch	−0.2 (1088)	−0.3 (298)	0.2 (511)	−0.7 (279) NS
Goldfinch	−0.2 (1087)	−0.7 (298)	−0.2 (512)	0.4 (277) NS
Linnet	0 (1087)	0 (298)	0 (512)	0 (277) NS
Yellowhammer	−1.2 (1088)	0 (298)	−1.4 (512)	−2.2 (278) NS

Table 2 The percentage local expansion of yellow wagtail and corn bunting in occupied 10-km squares between the two Atlas periods (1968–72 and 1988–91) in England and Wales, and in regions of predominantly arable, mixed and grassland agriculture. Local expansion was calculated as the number of squares occupied in 1988–91 but not in 1968–72, divided by the number of squares occupied in either period (i.e. losses are not included in the calculation); 10-km squares where a species was absent in both periods were omitted. Sample sizes (in brackets) indicate the number of occupied 10-km squares in either period. * $P < 0.05$, ** $P < 0.01$ (G-test)

Total 10-km squares	Overall change 1089	Arable 298	Mixed 512	Grassland 279	*P*
Yellow wagtail	9.7 (860)	13.1 (282)	7.0 (430)	10.8 (148)	*
Corn bunting	7.3 (782)	5.9 (269)	8.9 (390)	4.9 (123)	NS

shown that population changes have been greatest within this period for the majority of species. Maximum likelihood methods were used to provide a measure of model fit, testing whether annual changes were homogenous across sites (using χ^2 goodness-of-fit tests). In those cases where there was a good model fit (non-significant goodness-of-fit tests), population change was considered to be significant if confidence intervals did not overlap the reference index of 100%. In cases where there was poor model fit an estimate of relative population change is still presented, but confidence limits are not accurate and so nothing can be concluded about the accuracy of the estimated population change. Indices were also derived for different predominant farming types defined at the county level (Fig. 1).

RESULTS

Changes in bird distribution and species richness

Changes in species range were calculated as the ratio of the number of 10-km squares in which a species was present in the early atlas survey to the number in the late atlas survey. Overall percentage declines for the 20 selected species are shown in Table 1. Ten-kilometre squares were classified into predominantly arable, mixed and grassland agriculture (Fig. 1) (full details of national declines and distribution maps of all species are given in Gibbons *et al.*, 1993). Many of the 20 target species, while showing evidence of population declines, have not shown evidence of a contraction in range (Table 1). Seven species, all with a total range contraction of over 5%, showed significant differences between regions: grey partridge, lapwing, turtle dove, yellow wagtail, tree sparrow, corn bunting and reed bunting. Local extinctions were significantly greater in non-arable regions in all seven species (Table 1), and were greatest in the grassland region in each species except tree sparrow. The arable region showed the lowest rates of local extinction for each species, with yellow wagtail showing an expansion in this region. These differences were highly significant. Of the other species, although declines were small, a similar pattern was evident, with six species showing the greatest declines in the grassland region compared with three species in the arable region and no species in the mixed region. These analyses therefore indicate that local extinctions have been greatest in Wales and towards the north and west of England, regions dominated by grassland agriculture.

In the majority of species, the number of gains was very small. However, in two species, yellow wagtail and corn bunting, gains amounted to over 5% of all 10-km squares in which the species was recorded (Table 2) when only considering 10-km squares that had gained species between the two atlas periods (i.e. local extinctions were not included in the calculations). Yellow wagtail increased in a significantly greater proportion of 10-km squares in the arable region. However, there was no significant difference in the proportion of 10-km squares that had gained corn bunting between regions (Table 2).

Change in species richness was calculated as the difference in the number of species per 10-km square between the two atlas surveys, considering all species recorded, and 20 target species only. Figure 2 shows changes in species richness per 10-km square across the region. The areas showing the greatest loss of species tended to be in mixed and grassland regions. There was no significant difference in change in species richness between regions for all species (ANOVA $F = 1.73$, d.f. = 2,1086, NS; mean ± SD (n): arable 1.74 ± 10.47 species (298), mixed 0.54 ± 10.33 species (512), grassland 0.19 ± 11.78 species (279)), although there was a noticeable concentration of losses in the grass-dominated region of south-west England (Fig. 2a). There was a highly significant difference in species loss of target species between regions (ANOVA $F = 29.06$, d.f. = 2,1086, $P < 0.0001$; mean ± SD (n): arable –0.33 ± 1.12 species (298), mixed –0.72 ± 1.35 species (512), grassland –1.23 ± 1.77 species (279)). Species richness was also considered in relative terms (the ratio of species recorded in the old and new surveys per 10-km square), because species loss is in part a reflection of the number of species that are present initially. There was little difference in the pattern of percentage change in species richness of either all species or target species compared to absolute change. The significance of percentage change between different regions showed similar trends to absolute change (all species: $F = 2.29$, d.f. = 2,1086, NS; mean ± SD (n): arable 2 ± 13% (298), mixed 1 ± 12% (512), grassland 1 ± 15% (279);

(a)

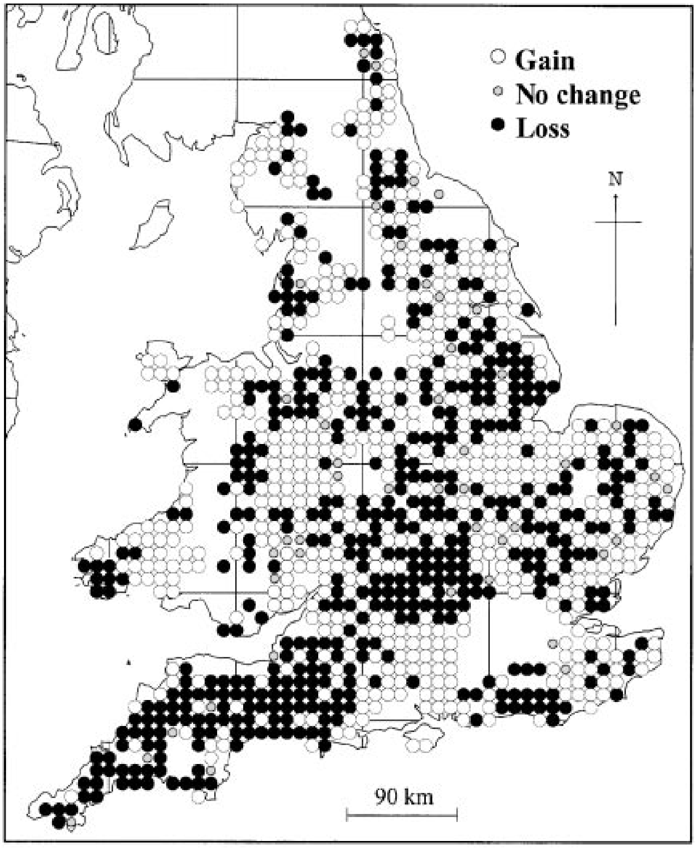

Fig. 2 Absolute change in species richness per 10-km square in lowland England and Wales between the two Atlas surveys; 10-km squares of less than 50% lowland farmland area are not included (blank regions on figures). (a) All species recorded, range of gains = 1–35 species, range of losses = 1–53 species; (b) 20 target species only, range of gains = 1–4 species, range of losses = 1–11 species.

target species $F = 35.59$, d.f. = 2,1086, $P < 0.0001$; mean ± SD (n): arable −2 ± 5% (298), mixed −4 ± 7% (512), grassland −7 ± 10% (279)).

Changes in abundance

Relative population changes for all plots and for regions of differing predominant farm type are given in Table 3. Considering overall population change, there were seven species that showed a significant population decline between 1970 and 1990, grey partridge, turtle dove, skylark, blackbird, song thrush, bullfinch and reed bunting. Two species, whitethroat and chaffinch, had increased significantly over the same period. There were poor model fits (significant heterogeneity between sites) in five species: lapwing, starling, tree sparrow, linnet and corn bunting. Even where models did not fit (Table 3), the estimated percentage declines were comparable to previously published estimates (Fuller *et al.*, 1995; Siriwardena *et al.*, 1998), the most notable exception being whitethroat, because the previously published work considered changes from the late 1960s onwards, a period when the whitethroat population was declining steeply due to changes in its African wintering habitat (Baillie & Peach, 1992). By 1970, the relative population size was very low, hence the large increases detected in Table 3.

Absolute decrease was greatest for seven species in arable regions (grey partridge, lapwing, blackbird, song thrush, tree sparrow, goldfinch,

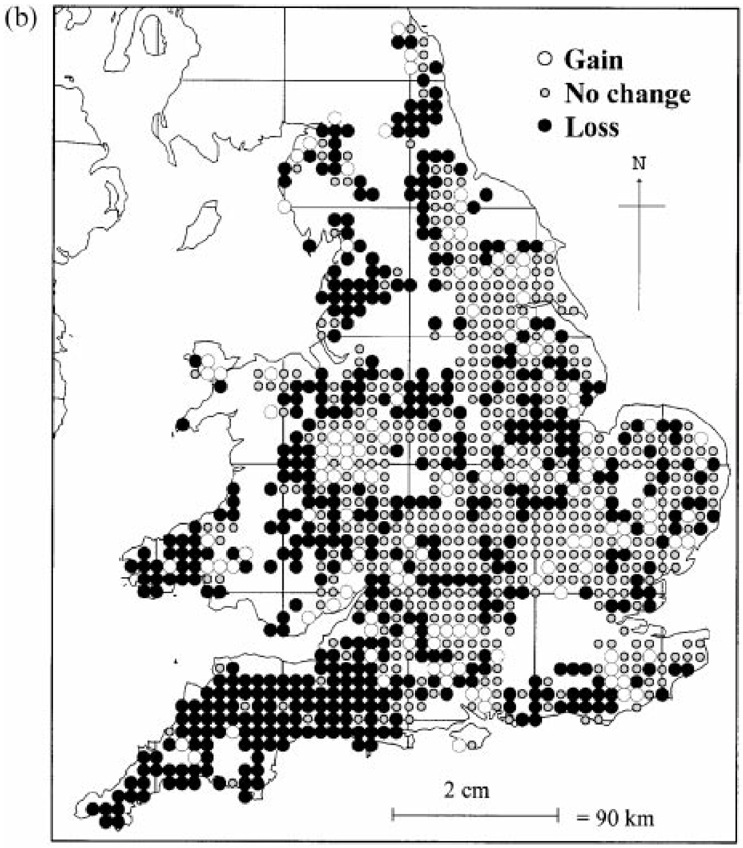

Fig. 2 *continued.*

and linnet), two species in mixed farming regions (corn bunting and yellowhammer) and nine species in grassland regions (kestrel, stock dove, turtle dove, skylark, yellow wagtail, starling, bullfinch, greenfinch and reed bunting). However, few of these species showed significant declines. Grey partridge, blackbird and song thrush had shown the greatest significant declines in arable regions and skylark, yellow wagtail, bullfinch and greenfinch had shown the greatest significant declines in grassland regions. One species had increased most on arable farmland (whitethroat), three had increased most on mixed farmland (stock dove, yellow wagtail and greenfinch) and three had increased most on grass farms (chaffinch, goldfinch and yellowhammer), but the change was significant in chaffinch only. Generally, species showed consistent trends between regions. The most notable exceptions were yellow wagtail and greenfinch which showed significant declines in grass-dominated farmland but (non-significant) increases in mixed farmland.

DISCUSSION

Population changes in relation to farming type

Of the seven species where local extinction at the 10-km square level showed significant regional differences, none showed a significantly higher rate of loss in the region characterized by arable farming. Although other individual species had shown very few local extinctions, declines in species richness of all species and of species associated with farmland were greater in the grass-dominated region. Changes in grassland systems have included increases in sheep numbers

Table 3 Population change of 20 selected target species on farmland in England and Wales between 1970 and 1990 over all sites and in regions of differing predominant agriculture. The number of sites indicates the total number included over the time span (not per year). Population indices were calculated using log-linear Poisson regression on CBC data. Goodness-of-fit was determined using maximum likelihood methods. Where goodness-of-fit was significant, confidence limits are not given. Significant population changes (non-significant goodness-of-fit and confidence interval not overlapping 100%) are indicated in bold type

Species	No. sites	Relative population change (%) ± 95% confidence limits			
		All plots	Arable	Mixed	Grassland
Kestrel	274	−16.0 ± 47.4	90.6 ± 226.6	−25.8 ± 59.3	−42.8 ± 69.7
Grey partridge	250	**−57.6 ± 13.9**	**−72.0 ± 21.4**	**−67.3 ± 17.5**	−20.8 ± 48.6
Lapwing	229	−38.9	−74.3	−60.7	−6.1
Stock dove	205	45.9 ± 54.6	39.3 ± 91.9	82.9 ± 95.0	−20.3 ± 80.3
Turtle dove	169	**−70.6 ± 11.9**	−66.6	−87.3	−99.0
Skylark	340	**−30.5 ± 7.6**	**−20.8 ± 15.4**	**−31.3 ± 11.9**	**−38.4 ± 13.2**
Yellow wagtail	134	4.5 ± 50.6	46.8 ± 179.3	108.9 ± 137.0	**−85.1 ± 16.0**
Starling	292	−33.8	−43.0	−36.2	−43.6
Whitethroat	300	**32.9 ± 29.8**	59.5 ± 61.9	41.3 ± 47.9	14.0 ± 57.2
Blackbird	367	**−32.2 ± 5.4**	**−38.8 ± 9.4**	**−37.2 ± 6.9**	−7.9 ± 16.9
Song thrush	349	**−63.9 ± 6.0**	**−70.8 ± 8.7**	**−69.9 ± 7.5**	**−32.1 ± 24.4**
Tree sparrow	222	−80.6	−85.8	−82.4	−70.5
Chaffinch	359	**29.2 ± 12.0**	**25.3 ± 24.5**	**26.0 ± 15.7**	**50.0 ± 31.6**
Bullfinch	259	**−69.1 ± 10.9**	**−53.9 ± 15.9**	**−64.0 ± 19.0**	**−78.9 ± 21.8**
Greenfinch	318	−13.0 ± 16.0	**−29.6 ± 22.0**	27.5 ± 35.4	**−46.3 ± 23.7**
Goldfinch	309	−0.5 ± 28.1	−36.3 ± 40.0	1.5 ± 37.6	53.0 ± 130.0
Linnet	314	−42.2	−58.2	−35.2	−31.4
Corn bunting	121	−78.4	−77.8	−78.2	−67.8
Reed bunting	237	**−23.4 ± 20.3**	−24.1 ± 41.6	−19.4 ± 33.2	−29.5 ± 34.8
Yellowhammer	303	−9.5 ± 12.9	−4.2 ± 22.6	−15.5 ± 18.0	3.9 ± 36.2

(Fuller & Gough, 1999), conversion of rough grazing to improved grassland, and increased rates of mowing silage facilitated by increased fertilizer application rates (O'Connor & Shrubb, 1986). The species most likely to be affected by these changes are ground-nesting birds such as lapwing, which may have been particularly affected by increases in stocking density (Beintema *et al.*, 1985; Shrubb, 1990; Chamberlain & Fuller, 2000), and yellow wagtail, which often nests in tussocky grass (Lack, 1992). For other species, potential effects of grass management on population size are less apparent. However, all species may have been affected by the increased polarization of grassland and arable farm systems, resulting in less arable cropping in grassland regions and a consequent decrease in habitat diversity (O'Connor & Shrubb, 1986).

Generally, there was no particular tendency for species populations to have declined most in any particular farming region. Grey partridge, blackbird and song thrush declines were associated particularly with arable farmland and skylark, yellow wagtail, bullfinch and reed bunting declines were associated particularly with grass farmland. These trends may indicate that management practices associated with particular types of farming are causing the population declines. For example, a strong link has been demonstrated between the management of arable farmland and population decline for grey partridge, which is due partly to increased herbicide applications eradicating food plants essential for invertebrate prey of the chicks (Potts, 1986). In this species, relative declines would therefore be expected to be more severe on arable-dominated farms. In grassland systems, ground-nesting species such as skylark and yellow wagtail may have been affected by intensification of grass management. However, for the other species there is no reason to suspect that declines should be particularly associated with a given farming type. Indeed, the decline of the skylark has been more commonly explained by changes in the management of arable crops, winter cereals being less suitable nesting habitat than the spring cereal that they have replaced (Chamberlain *et al.*, 1999).

Contrasting patterns according to distribution and abundance changes

Three species, turtle dove, yellow wagtail and reed bunting, showed the greatest decreases in abundance and the greatest local extinction rates in the grass-dominated region (although relative population change estimates were poor for turtle dove). Yellow wagtail also showed local expansion and increases in abundance in the arable region. For four species, grey partridge, lapwing, tree sparrow and corn bunting, there appears to be a contradiction between the results of the atlas analyses and those of the CBC data. In terms of distributional change, species losses (i.e. local extinctions at 10-km square level) have been least marked in arable-dominated areas. However, in terms of changes in abundance (CBC sites), the rates of population decline for these species have been greatest in arable-dominated areas. We suggest that a major cause may be that grass-dominated areas are essentially suboptimal for many farmland birds, at least in recent decades. Gibbons *et al.* (1993) present distribution maps derived both from point count data and from an 'abundance index' (actually a finer-scale measure of presence/absence that is correlated with species count) showing that by the late 1980s many lowland farmland birds were far less abundant in the west of lowland England and Wales than in the east. For example, this is the case for grey partridge, lapwing, turtle dove, skylark, linnet, tree sparrow, yellowhammer, reed bunting and corn bunting. Presumably for most species, these broad gradients in abundance would have been evident in the early 1970s because the CBC data indicate that population reductions of most species have occurred mainly in the eastern arable regions since the 1960s. Furthermore, several species are clearly associated with arable rather than grassland farming, e.g. grey partridge (Potts, 1986), skylark (Fuller *et al.*, 1997), yellowhammer (Kyrkos *et al.*, 1998). For many species, grass-dominated areas have probably long supported lower densities

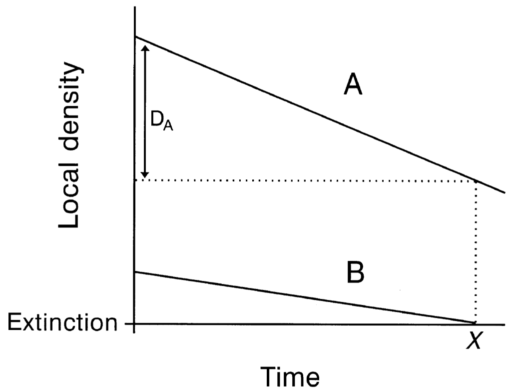

Fig. 3 Effect of initial density and rate of population decline on local extinction. A and B are two hypothetical species populations in different habitats with relatively high and low rates of decline, respectively, but population B is declining from a relatively low starting density and becomes extinct at a point, *X*, when the density of population A has merely declined by D_A. A and B could represent different predominant farming types (e.g. arable and grassland regions), or different species within a given region.

of several farmland birds than have mixed and arable-dominated areas. It follows, therefore, that a trend of modest reductions in numbers in grass-dominated areas but larger reductions in numbers in arable and mixed areas would lead to a preponderance of local extinctions in the former. This process is illustrated by a simple model in Fig. 3, where the lower initial abundance in the grass-dominated region leads to local extinction (and hence range decline), despite a steeper rate of decline in abundance in the arable/mixed region.

Figure 3 demonstrates how differing trends in abundance and distribution may arise in different regions, but other possible explanations may be operating simultaneously. In particular there are two aspects of agricultural change that are especially relevant. First, it is simplistic, even wrong, to assume that agricultural intensification has been most profound in the arable areas. There have been widespread fundamental changes in grassland management throughout much of lowland England in recent decades (Vickery *et al.*, 1999). These have resulted in considerable uniformity of management of lowland grassland with substantial associated increases in yield. The main changes have been widespread replacement of hay production by silage systems, with generally earlier and multiple cuts of grass. Inputs of inorganic fertilizers to grass have increased enormously, approximately doubling between 1970 and 1990 (unpublished data, British Survey of Fertilizer Practice). These are typically applied to all lowland grassland with the consequence that vegetation density in grasslands is far greater, but vegetation diversity is lower (Bunce *et al.*, 1998), than was the case several decades ago. There have probably been major implications for biodiversity associated with grassland systems but the subject has been little researched.

Secondly, the increasing polarization of agriculture towards grassland in western Britain and arable in eastern Britain may have had a disproportionate effect on farmland birds within the predominantly grassland areas. The reason is that many species are associated primarily with arable or mixed systems (see above) and these have become increasingly scarce in western Britain, which is now dominated by grassland (Chamberlain & Fuller, 2000). For example, skylark abundance is positively related to arable crop area (Fuller *et al.*, 1997) and although arable crops seem to be decreasing in quality for the skylark, it is still most abundant in south-eastern England (Browne *et al.*, 2000). The turtle dove may be the most extreme example of this effect, as it has decreased substantially in both range and abundance in western Britain and is now virtually extinct in the grass-dominated regions. Lapwings are more associated with grassland than the other species considered, but they also benefit from mixed farming (Hudson *et al.*, 1994), and this species has shown declines in grass-dominated areas where they were formally common (Wilson *et al.*, 2001). Finally, it is possible that source-sink dynamics (Pulliam, 1988) could be relevant, although there is no evidence that large-scale spatial dynamics of this kind are operating for farmland birds in Britain. This would require that populations in grassland areas are effectively maintained by immigration from more productive areas within the arable region. A population reduction in the latter area could lead to cessation of the emigration of 'surplus individuals'.

The findings of this paper indicate, first, that many lowland farmland birds are seriously declining in western Britain, and secondly, that the conclusions drawn from studies of distributional change will not always be the same as those drawn from studies of abundance change. Indeed, distribution change studies may actually give a misleading impression of the large-scale spatial dynamics of populations if information about abundance changes is unavailable.

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